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Robustness of trait connections across environmental gradients and growth forms

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Abstract

Aim: Plant trait databases often contain traits that are correlated, but for whom direct (undirected statistical dependency) and indirect (mediated by other traits) connections may be confounded. The confounding of correlation and connection hinders our understanding of plant strategies, and how these vary among growth forms and climate zones. We identified the direct and indirect connections across plant traits relevant to competition, resource acquisition and reproductive strategies using a global database and explored whether connections within and between traits from different tissue types vary across climates and growth forms.

Location: Global.

Major taxa studied: Plants.

Time period: Present.

Methods: We used probabilistic graphical models and a database of 10 plant traits (leaf area, specific leaf area, mass- and area-based leaf nitrogen and phosphorous content, leaf life span, plant height, stem specific density and seed mass) with 16,281 records to describe direct and indirect connections across woody and non-woody plants across tropical, temperate, arid, cold and polar regions.

Results: Trait networks based on direct connections are sparser than those based on correlations. Land plants had high connectivity across traits within and between tissue types; leaf life span and stem specific density shared direct connections with all other traits. For both growth forms, two groups of traits form modules of more highly connected traits; one related to resource acquisition, the other to plant architecture and reproduction. Woody species had higher trait network modularity in polar compared to temperate and tropical climates, while non-woody species did not show significant differences in modularity across climate regions.

Main conclusions: Plant traits are highly connected both within and across tissue types, yet traits segregate into persistent modules of traits. Variation in the modularity of trait networks suggests that trait connectivity is shaped by prevailing environmental conditions and demonstrates that plants of different growth forms use alternative strategies to cope with local conditions.

KEYWORDS
leaf traits, plant functional traits, plant strategy integration, seed traits, stem traits, trait interdependence, trait networks

1 | INTRODUCTION

Plant traits are not independent from each other biologically or statistically. An accurate description of their interdependency could give us a clearer view of a myriad of processes, from the links between morphological traits and physiological function inside the leaves of plants (Osnas, Lichstein, Reich, & Pacala, 2013; Poorter, Lambers, & Evans, 2014; Westoby, Reich, & Wright, 2013), to ecosystem-scale processes such as global gross primary production (Wang et al., 2012). Evidence of generalities in the coordination of traits exists, but it is mostly limited to single tissue types or a few traits at broad spatial scales (Chave et al., 2009; Moles et al., 2009; Wright et al., 2004), or across tissue types but only for certain regions and/or growth forms (Ackerly, 2004; Baraloto et al., 2010; Cheng, Chu, Chen, & Bai, 2015; Fortunel, Fine, & Baraloto, 2012; Freschet, Cornelissen, Logtestijn, & Aerts, 2010; Kramer-Walter et al., 2016; Liu et al., 2010). Díaz et al. (2016) found strong evidence for coordination among six traits measured on different tissue types at global scales, but they did not disentangle direct and indirect connections among traits. As of yet, it remains unknown how widespread coordination is among multiple traits across tissue types, and across different biogeographical scales and growth forms, once direct and indirect connections have been unravelled. By coordination, we mean variation in a trait that is linked to variation in another

trait or traits (i.e. non-random variation between traits). Crucially, in this paper, we try to disentangle the causal rather than correlative relationships that give rise to coordination or lack thereof among traits, and then assess whether this causal coordination among traits differs across biogeographical scales and growth forms.

Most previous studies describe the coordination across multiple traits using some form of correlative analyses (e.g. Ackerly, 2004; Freschet et al., 2010; Kramer-Walter et al., 2016). In this study, we instead focus on describing the causal coordination among traits by identifying their "connections". We use connection in a specific way: as short-hand for undirected statistical dependencies among traits (Shipley, 2016). A connection represents a direct linkage between two traits arising as a result of conditional statistical dependence among these traits (sometimes, and perhaps often, functional). That is, the observed correlation among these two traits cannot be fully explained by their connections to other traits. Meanwhile, indirect connections are due to conditional statistical independence among traits where no direct connection between the two traits exists, and any observed statistical correlation between them is indirectly mediated by both having connections to one or more other traits or by an environmental variable (see examples in Supporting Information Appendix S3). We note that we do not a priori believe that correlations that are due to covariances are unimportant physiologically or ecologically; in fact, they likely help to contribute to the small fraction of trait space that is occupied (Díaz et al., 2016) and thus of "trait strategies" that are successful in nature. However, distinguishing direct and indirect connections among traits is necessary for understanding the mechanistic roots of the trait correlations that define plant strategies, and can thus help us to clarify the causal link between traits and fitness components (Shipley, Lechowicz, Wright, & Reich, 2006), connections among traits and function (Li et al., 2015; Poorter et al., 2014), and the role that traits play in influencing higher-level processes and vegetation attributes (e.g. relative growth rate, net primary productivity, Kramer-Walter et al., 2016; Reich, Walters, & Ellsworth, 1992).

Highly connected traits are expected as a result of biophysical and/or selection processes that favour the efficient use and acquisition of resources within and across plant tissues (Reich, 2014). On the other hand, a certain degree of independence among traits can give plants more flexibility to adjust function to the environmental conditions currently experienced by the plant, and allow for more variation in the overall phenotype of the plant (Li et al., 2015; Messier, Lechowicz, McGill, Violle, & Enquist, 2017), as different traits/tissues have their own trade-offs. Li et al. (2015) found evidence for independence between the hydraulic and economic dimensions of leaves, which may give leaves more freedom to respond to existing environmental conditions. Meanwhile, Kramer-Walter et al. (2016) described coordination among root, stem and leaf tissue that also impacted plants relative growth rate (RGR), while also finding independent variation in specific root length (SRL), which may allow for higher phenotypic variation in roots compared to leaves. We should expect that interdependence among traits is mediated by evolutionary history, biophysical constraints, the environment that plants experience and whether selection favours the integration or independence of traits in those environments (Fortunel et al., 2012; Li et al., 2015; Messier et al., 2017; Reich, 2014).

While a number of studies have investigated the interdependence among traits across tissue types (e.g. Ackerly, 2004; Fortunel et al., 2012; Kramer-Walter et al., 2016; Messier et al., 2017; Reich, 2014), only a handful have done so at macroecological scales. At a global scale, Díaz et al. (2016) showed plant species occupy two orthogonal trait dimensions across six traits; one dimension, related to the size of plants, was formed by seed mass and stem traits, and the other dimension was composed of leaf traits that characterize the construction costs of photosynthetic tissue. Leaf and stem traits of Neotropical trees have also been shown to vary independently of each other (Baraloto et al., 2010). Meanwhile, interdependence among leaf, stem and root traits of trees in New Zealand has been shown (Kramer-Walter et al., 2016), as well as among traits across tissue types in Mongolian grasslands (Cheng et al., 2015), and northern European herbaceous species (Kleyer et al., 2018). Thus, there seems to be evidence for high interdependence among traits across tissue types; however, this seems to be variable across environments and growth forms and to be highly dependent on the traits examined. As of yet, it remains unclear how the causal interdependence of traits varies globally, across biogeographical scales and among plant groups.

Water availability is likely to influence the amount of interdependence among different tissues types. Plant communities from wetter environments exhibit independence among leaf, root and stem tissue types (Baraloto et al., 2010; Fortunel et al., 2012; Jager, Richardson, Bellingham, Clearwater, & Laughlin, 2015), while in drier environments interdependence among these tissue types has been observed (Laughlin, Leppert, Moore, & Sieg, 2010; Li & Bao, 2015; de la Riva et al., 2016). Similarly, the independence of traits related to water acquisition from traits related to nutrient acquisition increases in environments with higher precipitation (Ackerly, 2004; Baraloto et al., 2010; Fortunel et al., 2012; Ishida et al., 2008), and with increasing water availability (de la Riva et al., 2016). Thus, higher connectivity among traits may be selected for in drier environments or in environments with higher seasonal variation in water availability, as matching tissue strategies may allow the plants to function efficiently (Reich, 2014) and take up resources faster when conditions allow. Following this, we hypothesized that arid and polar/cold climates – where water availability is limited throughout most of the year or is available during a short season– will favour more connectivity across traits.

Numerous studies have described multi-trait interdependence among woody species (e.g. Ackerly, 2004; Baraloto et al., 2010; de la Riva et al., 2016; Jager et al., 2015; Li & Bao, 2015), while fewer studies have done so across non-woody species (e.g. Cheng et al., 2015; Craine, Froehle, Tilman, Wedin, & Chapin, 2001; Craine & Lee, 2003; Santini et al., 2017). To our knowledge, only Diaz et al. (2016) have specifically contrasted the difference in coordination among different traits across tissue types among woody and non-woody species, finding no difference in trait interdependence between growth forms, but some differences in the strength of specific trait correlations. Despite these efforts, differences in trait interdependence in woody and non-woody species still remain unexplored.

Several recent studies at local to regional scales have made more comprehensive examinations of multi-trait integration for either herbaceous or woody plants. For example, Kleyer et al. (2018) and Messier et al. (2017) explored trait integration within a growth form, employing higher trait resolution than typically done previously (i.e. their studies incorporated all vegetative tissues and sometimes even reproductive tissue types and > 20 traits). These studies both suggested that traits integrate by function rather than by tissue type, and also identified traits with high interdependence levels (we refer to these as traits with high centrality). Both traits also found evidence for interdependence among traits across tissue types with no clear-cut segregation of traits into distinct trait dimensions. While neither study quantified the connectedness of the whole trait network (what we refer to as the edge density of the network), a quick calculation using their reported numbers of observed trait connections divided by the number of possible connections suggests that the trait network of non-woody species (65 present connections/210 possible connections; Kleyer et al., 2018) is similar but perhaps slightly more connected than woody species (41 present connections/190 possible connections; Messier et al., 2017). However, this calculation and other comparisons among these studies are complicated by dissimilarities in spatial scales and suites of targeted traits. There is very limited knowledge available that directly addresses the differences/similarities in trait interdependence between growth forms; however, from the limited evidence available, we hypothesized that non-woody species may display higher interdependence among traits.

Here we explore three hypotheses: (a) that trait connections (i.e. undirected statistical dependencies) and trait correlation are identical, (b) that high trait connectivity will be favoured in biomes where water availability is limited such as in arid and polar/cold climates, and (c) that trait connectivity will be higher in non-woody than woody species. To address our hypotheses we (i) compare trait correlations and trait connections for each pair of traits in our trait network; (ii) describe the global trait network based on the connections between 10 functional traits using 16,281 trait observations from sites around the world; (iii) use network metrics to compare the differences in the trait networks of woody and non-woody species; and to (iv) assess how the trait networks of woody and non-woody species change across five broad climate regions (tropical, temperate, arid, cold and polar). We evaluate the connections among traits through a test of undirected statistical dependence using a structure learning algorithm using the well-studied graphical Lasso (Friedman, Hastie, & Tibshirani, 2008). The key feature of this method is its capacity to identify direct from indirect connections with high probability by identifying relationships among traits once covariation with all other traits has been accounted for.

2 | METHODS

2.1 | Trait, taxonomic data and climate zones

Our attention is on 10 plant traits related to the functions of leaf tissues, stem tissues, and reproductive tissues of plants, and are thus relevant to resource economy and uptake, competitive ability (or stress tolerance) and reproductive strategy. Seed mass (mg) reflects allocation of energy to few large versus many small offspring, and impacts early seedling survival (Moles & Westoby, 2006). Plant height (m) and stem specific density (mg dry mass/mm^3 fresh volume; hereon SSD) are related to light competition, growth rate and long-term viability of stems (Chave et al., 2009; Moles et al., 2009). Specific leaf area (mm^2/mg; SLA), leaf life span (month; LLS), leaf nitrogen (mg/g; N) mass and leaf phosphorus (mg/g; P) mass are related to nutrient economy and acquisition, and are key components of the leaf economic spectrum (LES; Reich et al., 1999; Wright et al., 2004). SLA represents the potential return rate measured in terms of light capture area per unit of mass investment (Reich, Walters, & Ellsworth, 1997; Wright et al., 2004). LLS represents the time needed to generate payback on this investment (Reich et al., 1992). Leaf N is associated with carboxylation capacity and is integral to the photosynthetic machinery (Reich et al., 1999; Wright et al., 2004). Leaf P is essential for bioenergetic molecules (e.g. ATP) and is linked to the formation of indispensable nucleic acids and lipid membranes (Reich et al., 1999; Wright et al., 2004). Therefore, variations in leaf P and N are crucial to respiration and photosynthetic capacity, as well as energy generation and storage. Leaf area (mm^2) is related to the water and energy balance of a plant and is relevant to light interception. Finally, leaf N and P can also be expressed on an area basis (g/m^2) reflecting light capture and transaction of energy on an area basis (Wright et al., 2004). Consequently, we also use leaf N per area and leaf P per area, in parallel to their mass-based counterparts.

We obtained spatially explicit trait data for our 10 traits and growth form (woody, non-woody) data from TRY (www.try.db.org; Kattge et al., 2011; a list of the original data sources is found in the Appendix). The TRY data subset used in this study includes 16,281 georeferenced trait observation records for 15,284 species, of which 9,053 and 6,231 species were identified as woody and non-woody plants, respectively. When we had multiple observations for the same trait for a species within the same climatic region, we used the geometric mean to calculate a single species–climate region combination, with the exception of plant height, for which we used the maximum value. We standardized the species names to *The Plant List* (v. 1.1; The Plant List, 2013), and obtained the higher order taxonomy for our species with taxonlookup (v. 1.0.1; Pennell, FitzJohn, & Cornwell, 2016). In our dataset LLS was the trait with the lowest number of records (*c.* 0.67% of records have information for this trait), while plant height was the trait with the highest number of records present (*c.* 35%; Supporting Information Table S1.1. Thus, we used a hierarchical Bayesian extension of probabilistic matrix factorization (BHPMF) to fill in the trait gaps in our dataset (Fazayeli, Banerjee, Kattge, Schrodt, & Reich, 2014; Schrodt et al., 2015; Shan et al., 2012). This algorithm harnesses the available trait and taxonomic information to fill in the gaps in the trait data, by approximating the trait matrices at higher taxonomic levels, which then serve as priors for the next level in the hierarchy (Fazayeli et al., 2014; Schrodt et al., 2015). This approach has the advantage of leveraging any phylogenetic signals in traits, although a phylogenetic signal is not a prerequisite for the model to work efficiently (Schrodt et al., 2015).

Previous studies have evaluated BHPMF's prediction accuracy, uncertainty, and confidence in predictions. These studies have compared BHPMF to other methods such as probabilistic matrix factorization and the more commonly used MEAN – gap-filling with species or genus level mean values – using plant traits datasets spanning 49–92% missing entries per trait (Fazayeli et al., 2014; Moreno-Martínez et al., 2018; Schrodt et al., 2015). BHMPF's prediction accuracy outperforms all other methods with lower root mean square error (RMSE) values, and higher correlation coefficient of observed versus predicted values (Fazayeli et al., 2014; Schrodt et al., 2015). BHPMF's average error of predictions is about half a standard deviation, and crucially its prediction accuracy is not related to the number of entries per trait (Schrodt et al., 2015). BHPMF preserves trait–trait correlations well and reproduces extreme values more accurately than MEAN, thus it also captures the shape of the scatter of observed trait data more accurately than MEAN (Schrodt et al., 2015). Further, uncertainty evaluation tests based on the relationship between a model's confidence versus accuracy have shown that BHPMF is accurate when confidence is high (Fazayeli et al., 2014; Schrodt et al., 2015). By contrast, MEAN can introduce large error and bias in some cases as this method adds new data points without adding new information, making confidence limits incorrect (Fazayeli et al., 2014; Schrodt et al., 2015).

A number of studies have used the BHPMF method in other trait analyses with robust results (see Blonder et al., 2018; Caplan, Meiners, Flores-Moreno, & McCormack, 2018; Díaz et al., 2016; Moreno-Martínez et al., 2018). Nonetheless, we also checked the robustness of the BHPMF algorithm by comparing the trait–trait relationship from 1,000 gap-filled datasets versus trait–trait correlations only from the original dataset (Supporting Information Figure S1.1, and determining the correlation between the accuracy (RMSE) and confidence (*SD*) of the algorithm using our dataset (Supporting Information Figure S1.2. The first test shows that BHPMF reproduces extreme values accurately capturing the shape of the scatter of observed trait data and in most cases the original trait–trait correlation lies inside the 95% confidence interval of the 1,000 gap-filled datasets suggesting the algorithm is robust in assessing correlations among trait pairs (Supporting Information Figure S1.1. The relationship between RMSE and *SD* suggests that the algorithm is accurate when it is confident (Supporting Information Figure S1.2. Further, we ensured the robustness of our results by re-running our analyses excluding LLS, which is the most gap-filled trait in our dataset (Supporting Information Appendix S1).

Using a map of the Köppen climate zones we assigned the georeferenced plant records to five different climates: tropical climate (with little to moderate water deficiency through seasons), which includes tropical rainforest, tropical seasonal forest, and savannas; arid climate (with low water availability through seasons), which includes deserts and steppes; temperate climate (with little or no water deficiency through seasons and seasonal variation in temperature), which includes temperate forest, temperate rainforest and Mediterranean vegetation; cold climate (with low water availability and high temperature seasonality), which includes only taiga; polar climate (with low water availability and extreme variation in temperature), which includes tundra, alpine and circumpolar zones (Peel, Finlayson, & McMahon, 2007). While variation in temperature and/or water availability exist within these climate regions, more variation in environmental conditions occurs among them (Peel et al., 2007). We chose the climate types above for two reasons: (a) the climate types described above are based on long-term precipitation and heat records, which combined capture broad thermal and moisture differences among regions (Feddema, 2005), (b) the sparsity of plant trait data at global scales precludes the use of the 30 Köppen climate subtypes described by Peel et al. (2007).

2.2 | Estimation of trait correlations

We used Pearson correlations to calculate the relationship for each trait pair across all land plants. To estimate the statistical significance of the correlations, we generated 1,000 bootstrapped trait datasets and calculated the 95% confidence interval of the correlation for each trait pair. To determine the relationship between correlation and connections (the derivation of these is described below) we compared their absolute value for each trait pair, since we did not have a hypothesis about the sign of these metrics. Prior to analyses we $\log_{10}$ transformed and *z*-transformed all continuous trait data.

2.3 | Estimation of trait connections

To determine the connections among traits we calculated the precision matrix and the confidence interval for each trait–trait interaction in the trait network. The precision matrix (i.e. inverse of the covariance matrix) establishes the undirected statistical dependency among a set of variables, in this case a set of traits. Undirected statistical dependencies can be understood in terms of partial correlations. Given a pair of traits (*x* and *y*) with correlation $\rho = \rho_1 + \rho_2$, ρ_1 would be how much of this correlation can be explained by another trait *z* (*z* being a single trait or set of traits), while ρ_2 would be how much of this correlation cannot be explained by *z*. Here, ρ_2 is the partial correlation and would correspond to an entry in the precision matrix for the undirected statistical dependency between traits *x* and *y*. If $\rho_2 = 0$, then any observed correlation between traits *x* and *y* can be fully explained by *z* (i.e. traits *x* and *y* do not provide information about each other once trait *z* is considered). If $\rho_2 \neq 0$, then there is a direct connection between traits *x* and *y*, even after accounting for trait *z*. Thus, the precision matrix of traits provides the undirected statistical conditional dependency structure among traits for a multivariate (in this case, assumed log-normal) set of traits, which describes the direct probabilistic interactions among traits (Supporting Information Appendix S2; Cai, Li, Liu, & Xie, 2012; Ebert-Uphoff & Deng, 2012). Importantly, the sparsity structure of the precision matrix matches the sparsity structure of ρ_2.

We derived the precision matrix for all plants, and then for non-woody and woody plants separately. Next, we derived the precision matrix for non-woody and woody plants within each of the five climate zones defined above. We used a "glasso" algorithm (Graphical Lasso; Friedman et al., 2008) to estimate the precision matrix for each plant group. The glasso algorithm assumes that traits have a

multivariate Gaussian distribution and estimates the precision matrix by minimizing the negative log-likelihood among all plant trait measurements. Following Jankova and van de Geer (2015), we accounted for differences in sample size across precision matrices and their effect as: $\lambda = 2\sqrt{(\log p/n)}$, where n refers to the sample size and p denotes the number of variables (i.e. traits; Supporting Information Appendix S2). Then for each precision matrix, we tested the significance of the trait–trait connections using a glasso-based confidence interval (Jankova & van de Geer, 2015). Finally, we removed the connections among traits whose confidence interval contained zero.

2.4 | Characterization of networks of trait connections using network metrics

To characterize the differences in the connections among traits – which were obtained through the estimation of precision matrices – within and across trait networks, we used three common metrics in the analyses of networks: "modularity" to establish the connectivity among trait modules, "edge density" to quantify the connectivity of all traits across the whole trait network, and "degree" to quantify the connectivity of a focal trait to other traits in the network. We describe each of these metrics in detail below.

"Modularity" is the difference between the fraction of connections among traits that fall within a given module (i.e. a module is a subset of traits that interact more among themselves than with other surrounding traits) minus the same fraction in a null model where connections among traits are randomly distributed (Clauset, Newman, & Moore, 2004; Figure 1). We used modularity to measure the connectivity among trait modules. Modularity helps identify the tendency for traits within a trait network to cluster, in that networks with high modularity have a great number of connections among traits within modules but sparse connections among traits between modules (Figure 1). Higher modularity of traits confers an advantage under variable conditions as it lends robustness (Alon, 2003; Ravasz, Somera, Mongru, Oltvai, & Barabási, 2002), also providing opportunities for the network to adapt and evolve, as not all components

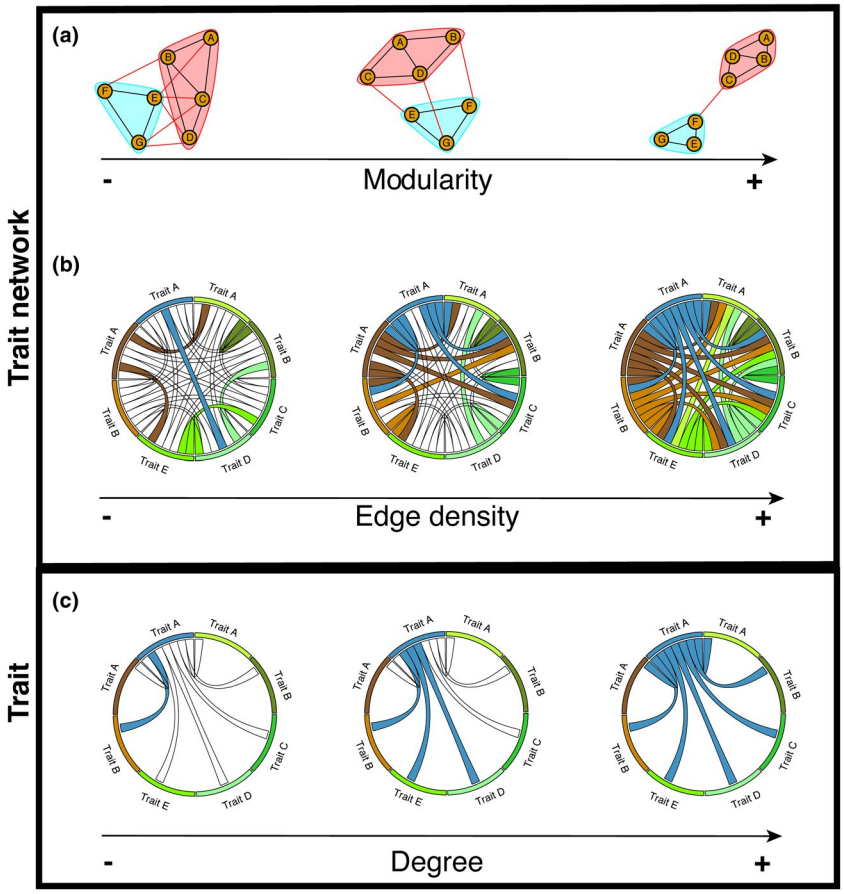

FIGURE 1 Network metrics used to assess the causal interdependence (i.e. connections) among traits. The metrics focus on the trait network, and individual traits' properties. *Modularity*: describes the tendency of nodes within a network to cluster by quantifying how separated modules within a network are from each other. Modules are groups of traits (blue and red polygons) that interact more strongly among themselves than with other traits. In networks with low modularity traits interact strongly among modules (panel a, left), in networks with high modularity (panel a, right) traits within a module interact more strongly among themselves than with traits in other modules. *Edge density*: proportion of present connections among traits out of all possible connections in the network. In networks with high edge density (panel b, left), connections exist between all traits, networks with low edge density (panel b, right figure) have few connections among traits. *Degree*: measures how many connections an individual trait (e.g. Trait A) has with other traits in the network. A trait with high degree has connections with many (sometimes all) other traits (panel c, left) in the network, a trait with low degree (panel c, right) has no or few connections with other traits in the network

in a modular network are optimally linked (i.e. ability to respond to changing external conditions/internal organization while maintaining normal behaviour; Barabasi & Oltvai, 2004). We used a Spinglass algorithm to detect the module placement in our networks. To identify module placement this algorithm is based on the principle that nodes should connect edges of the same community, while nodes of different communities should be disconnected (Yang, Algesheimer, & Tessone, 2016). The community detection through spin glass may be understood as finding the ground state of an infinite range Potts spin glass by combining the information from both present and missing links (Reichardt & Bornholdt, 2006). The network community structure is interpreted as the spin (i.e. community) configuration that minimizes the energy of the spin glass, where the spin states are the community indices. The Spinglass algorithm accurately detects modules in networks of small size (number of nodes – here, traits – ≤ 233) and with small or large mixing parameters at the network level (i.e. the summation of external degree of each node over the summation of its total degree; Yang et al., 2016). Once we determined the placement of modules in the networks, we recorded the number of modules present, their trait composition and calculated their modularity. Modularity values of zero represent networks without compartmentalization of modules (i.e. networks where there is no subset of traits that interact more among themselves than with other surrounding traits), while non-zero values represent networks that have compartmentalization of modules (i.e. networks that tend to have dense connections among traits within modules but sparse connections to traits in other modules; Figure 1).

"Edge density" defines the proportion of present connections among traits out of all possible connections in a trait network (Figure 1). We used edge density to assess the connectedness across traits of the whole trait network, regardless of their modules. In the context of biological networks, variation in edge density is used as an indicator of the compromise between efficiency of connections versus the cost of connections (Alon, 2003; Lipson, Pollack, Suh, & Wainwright, 2002). For instance, a network with high edge density may allow for the efficient acquisition and mobilization of resources (as all traits are connected with all other traits), nevertheless this may be costly in terms of the establishment and maintenance of connections among traits. Edge density ranges from zero to one. A value of zero represents no connection across the traits in the network; a value of one implies that all traits in the network are connected to all other traits (Figure 1).

"Degree" is the number of connections between a focal trait and other traits, normalized by the total number of potential connections (Horvath, 2011; Figure 1). This is a measure of the connectivity of a focal trait to the rest of the trait network. Thus, we used degree – a type of centrality measure – to quantify the relative importance (the centrality) of a trait for a given trait network; values for degree range between zero when a focal trait has no connection to any other trait, to one when a focal trait is connected to all other traits in the network. Degree is widely used in biological networks to identify essential characteristics in biological entities such as genes, metabolites and proteins (Koschützki & Schreiber, 2008). For example, metabolites with higher degree may belong to the oldest part of the metabolism, while proteins with higher degree have been identified as essential, with their removal being lethal to the organism (Koschützki & Schreiber, 2008).

2.5 | Significance of differences in trait network metrics

To estimate the statistical significance of the differences in network metrics above), we did the following: First, using 1,000 bootstrapped trait datasets, we calculated the precision matrices for each plant group and climate region (as described above), and calculated each network metric for each of the 1,000 resulting trait networks. Then, for a given network metric (i.e. modularity, degree, edge density) we calculated the 95% confidence interval of the difference across all group pairs. Following Besag, Green, Higdon, and Mengersen (1995), we corrected for multiple comparison by calculating simultaneous credible intervals based on order statistics of the difference in a given network metric among groups.

We ran all analyses in R 3.5.3 (R Core Team, 2019). For calculating the precision matrices we used the camel package (Li, Zhao, & Liu, 2013), and for calculating the network metrics we used the igraph package (Csardi & Nepusz, 2006).

3 | RESULTS

Contrary to our first hypothesis, we found that trait connections and trait correlation are not identical for all land plants (Figure 2). From the 28 unique trait–trait relationships possible in our trait networks, we found that 23 have both significant trait–trait correlations and trait connections, four have only significant trait correlations and one has only a significant trait connection (Figure 2c,d, Supporting Information Table S4.1. The disagreements between connections and correlations occur in trait–trait relationships with medium to low correlation values ($|r| <= .30$; Figure 2d). There is a connection between leaf N mass–seed mass, but no correlation between these traits. On the other hand, there are four trait–trait relationships with significant correlations (leaf P mass–seed mass, leaf N mass–plant height, leaf area–leaf P mass and leaf area–leaf N mass), but without significant connection among these traits (Figure 2c). We found that strong correlations, such as those between SLA–LLS, seed mass–plant height, leaf N mass–leaf P mass ($|r| >= .5$), were always present as connections (Supporting Information Table S4.1.

Among all terrestrial plants, there is a high proportion of connections among traits across all tissue types (edge density = .86, Figure 3a and Supporting Information Figure S4.1), and no modularity among traits (modularity = 0, Figure 3b). LLS and SSD (both degree = 1) are more central to the global trait networks in that they have significantly higher numbers of connections to other traits compared to plant height (degree = .86), leaf N (degree = .71) and leaf area (degree = .71). Leaf area (degree = .71) and leaf N mass (degree = .71) are the traits with the fewest connections to other traits (Figure 3c and

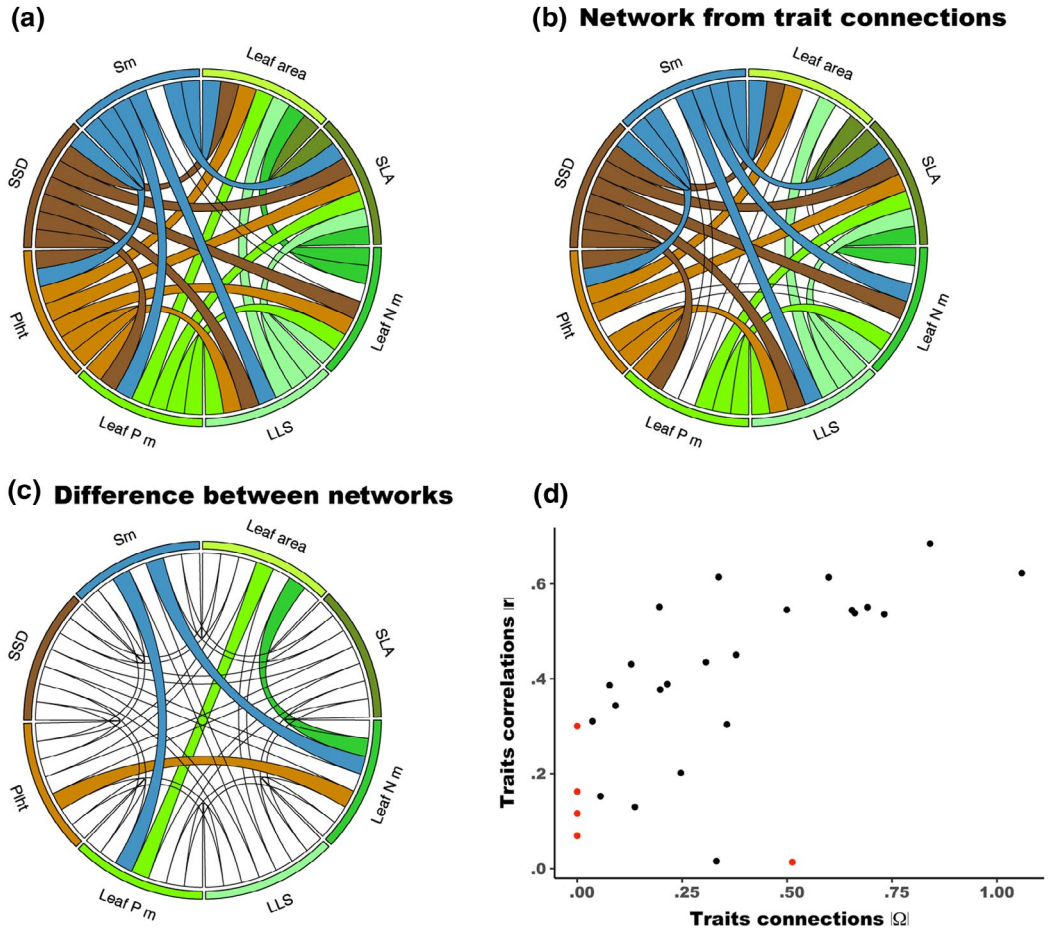

FIGURE 2 Comparison of trait correlations (*r*) and connections (Ω). (a) Trait network based on correlations (coloured connections are significant). (b) Trait network based on connections (coloured connections are significant). (c) Trait connections that differ from correlations. (d) Comparison of absolute values of trait connections and correlations; black points are significant trait–trait correlations and significant trait connections, red points are trait-trait relations that had either connections or correlations that were not significant

Supporting Information Table S4.2, S4.3. All other traits fall somewhere in between these two extremes, in descending order: SLA also had a high proportion of connections to other traits, but only significantly higher than plant height and leaf N; seed mass had higher proportion of connections to other traits but only compared to leaf N; and leaf P had a low proportion of connections compared to other traits; however, this difference was not significant (Figure 2c and Supporting Information Table S4.2, S4.3. Details of the global trait networks and multiple comparison corrected 95% confidence intervals for all results are in Supporting Information Appendix S3.

Contrary to our hypothesis that non-woody species will have higher connectivity among traits compared to woody species, we found that both growth forms have similar proportions of connections among traits in the trait network (edge density$_{woody}$ = .71; edge density$_{non\text{-}woody}$ = .61; Figure 3a and Supporting Information Figure S4.1) and both have two trait modules with comparably low levels of modularity, showing higher integration of traits across modules than within modules (modularity$_{non\text{-}woody}$ = .10; modularity$_{woody}$ = .06; Figure 3b). However, we found some fundamental differences in the composition of the trait modules and in the identity of most central traits in the trait networks. In terms of the modules' composition, in non-woody species one module is composed of LLS, leaf N and SSD, while the other is composed of leaf P, SLA, plant height, leaf area and seed mass (Table 1). Meanwhile, in woody species one module is formed by leaf area, leaf P and SSD and the other one by seed mass, LLS, SLA, leaf N and plant height (Table 1). Both growth forms have comparable levels of modularity, showing higher integration of traits across modules than within modules (modularity$_{non\text{-}woody}$ = .10; modularity$_{woody}$ = .06; Figure 3b). For non-woody species leaf N, leaf area, LLS and leaf P (degree = .71) are the traits with the highest number of connections to other traits in the trait network (Figure 3d). Meanwhile, for woody species the traits with the highest proportion of connections to other traits are LLS (degree = .86), leaf area (degree = .86) and seed mass (degree = .86, Figure 3e). In both cases stem-related traits are the traits with the fewest connections to other traits in the network (degree ≤ .57 Figure 3d,e). Details on trait networks of woody and non-woody species are presented in Supporting Information Appendix S3.

In both woody and non-woody species, there are connections among all leaf-tissue traits, except SLA–LLS in non-woody species.

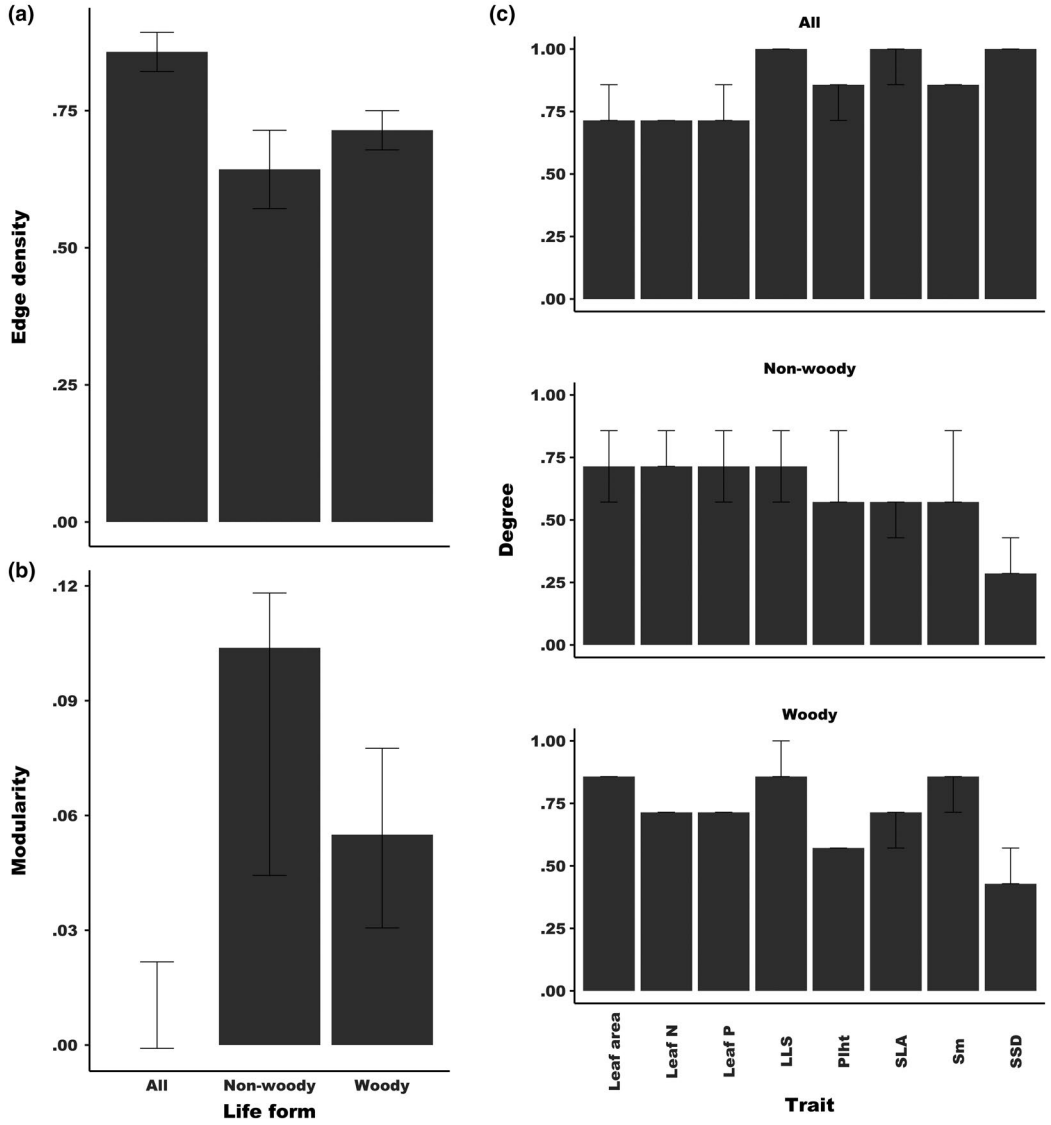

FIGURE 3 Trait networks for all plants, woody and non-woody growth forms. (a) Edge density, (b) modularity and (c) trait degree. Whiskers denote 95% confidence interval. See Figure 1 for hypothetical graphical examples of these metrics

TABLE 1 Modules' composition for all plants, non-woody and woody species

Growth form	Modules
All plants	Leaf area–SLA–leaf N–LLS–leaf P–plant ht–SSD–seed mass
Non-woody	Leaf area–leaf P–plant ht | SLA–leaf N–LLS–SSD–seed mass
Woody	Leaf area–LLS–plant ht–seed mass | SLA–leaf N–leaf P–SSD

Note: plant ht = plant height; LLS = leaf life span; SLA = specific leaf area; SSD = stem specific density. Modules in our networks are detected using the Spinglass algorithm (see Methods). The modules in this table are the most common modules across the 1,000 networks obtained from the analyses of 1,000 bootstrapped trait matrices. The pipe character "|" separates individual modules. Traits across modules may be connected (see graphical representation of modularity in Figure 1b); however, they tend to be more connected with other traits within the modules than with traits outside the module.

Also, in both growth form groups there are connections between plant height–leaf area, plant height–LLS, seed mass–leaf area, seed mass–SLA, seed mass–leaf N and seed mass–plant height. Connections between LLS–SLA, SSD–leaf area, SSD–leaf P, plant height–leaf N, seed mass–LLS, and seed mass–SSD are only present in woody species. Connections between SSD–leaf N, SSD–LLS and plant height–leaf P are only present in non-woody species.

3.1 | Woody and non-woody species by climate region

Connections among traits of woody and non-woody species differ across climate regions (Supporting Information Figure S4.2. However, contrary to our expectations, the proportion of connectedness among traits did not increase with decreasing water availability. Woody species show a higher proportion of connections among traits (i.e. higher edge density) in tropical (edge density = .64),

temperate (edge density = .68), arid (edge density = .64) and cold environments (edge density = .57), compared to polar ones (edge density = .39; Figure 4a and Supporting Information Figure S4.2, Table S4.4, 4.5. Non-woody species show a higher proportion of connections between traits in cold (edge density = .61) compared to polar environments (edge density = .43; Figure 4c and Supporting Information Figure S4.2, Table S4.4, 4.5). However, non-woody species also have a higher proportion of connections in temperate (edge density = .57) and cold environments compared to tropical environments (edge density = .36; Figure 4c and Supporting Information Figure S4.2, Table S4.4, 4.5).

Woody species show significantly higher integration of traits within modules in polar (modularity = .25) compared to temperate and tropical environments (for both modularity = .08; Figure 4b and Supporting Information Table S4.6, 4.7). Non-woody species show non-significant differences in modularity across environments (Figure 4d and Supporting Information Table S4.6, 4.7). Across the different climate regions, woody species always have two modules, while non-woody species have two modules in all climates except polar and tropical where they have three (Table 2). Both growth forms have a module mainly composed of traits related to the LES. In woody species, this consists of leaf N and leaf P, and SLA is part of this module in all climates except tropical, while LLS is part of this module in all climates except cold climate. In non-woody species, the analogous module contains SLA, leaf N and leaf P in all climate regions. The second module consists of traits related to reproductive strategy and plant architecture for woody species, and mainly plant architecture in non-woody species. In woody species, the core traits in this module are seed mass, plant height, leaf area and SSD. In non-woody species this module consists of plant height and leaf area; SSD is part of this module in all climates except polar, and seed mass is part of this module in all climates except tropical and arid. When a third module is present in non-woody species, it consists of LLS and either plant height in tropical, or SSD in polar climates (Table 2).

For both growth forms, LLS is the trait with the highest centrality (i.e. it has the most connections to other traits) in temperate ($degree_{woody}$ = .71, $degree_{non\text{-}woody}$ = .71) and arid climates ($degree_{woody}$ = .86, $degree_{non\text{-}woody}$ = .57), while seed mass has high centrality in tropical areas ($degree_{woody}$ = .86, $degree_{non\text{-}woody}$ = .43; Supporting Information Table S4.8–4.11). For non-woody species leaf N has a high centrality in all climate zones, except cold, while leaf area has a high centrality in all environments except temperate and polar ones (Supporting Information Table S4.10, 4.11). For woody species LLS has the highest centrality in all regions except tropical ones (Supporting Information Table S4.8, 4.9).

Across climate types and both growth forms, connections between leaf N–leaf P, leaf N–SLA, plant height–leaf area and seed mass–leaf area are always present. For non-woody species connections among seed mass–SLA and seed mass–leaf N are also robust across climate types. Meanwhile, for woody species connections between SLA–leaf area, leaf P–SLA, LLS–leaf N, SSD–leaf P, seed mass–plant height and seed mass–SSD are also found across climate regions. Details of trait network differences across climate regions are presented in Supporting Information Appendix S3.

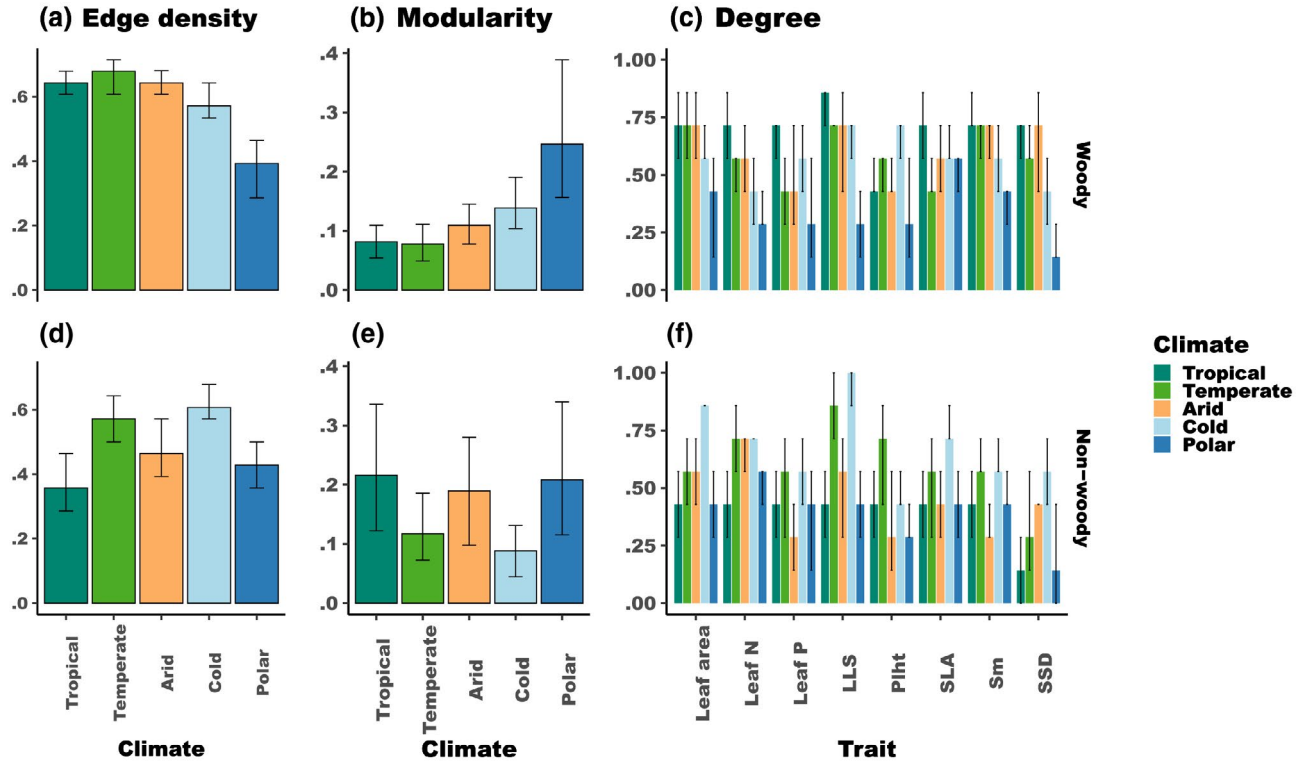

FIGURE 4 Plant trait network edge density, modularity, and trait degree for woody (a, b and e, respectively) and non-woody species (c, d and f, respectively) across five climate regions using mass-based leaf N and P. Whiskers denote 95% confidence interval

TABLE 2 Modules of non-woody and woody species across climate regions

Climate	Woody species modules	Non-woody species modules
Tropical	Leaf area–SLA–plant ht–SSD–seed mass | leaf N–LLS–leaf P	Leaf area–SSD | SLA–leaf N–leaf P–seed mass | LLS–plant ht
Temperate	Leaf area–plant ht–SSD–seed mass | SLA–leaf N–LLS–leaf P	Leaf area–LLS–plant ht–SSD–seed mass | SLA–leaf N–leaf P
Arid	Leaf area–plant ht–SSD–seed mass | SLA–leaf N–LLS–leaf P	Leaf area–LLS–plant ht–SSD | SLA–leaf N–leaf P–seed mass
Cold	Leaf area–LLS–plant ht–SSD–seed mass | SLA–leaf N–leaf P	Leaf area–LLS–plant ht–SSD–seed mass | SLA–leaf N–leaf P
Polar	Leaf area–plant ht–SSD–seed mass | SLA–leaf N–LLS–leaf P	Leaf area–plant ht–seed mass | SLA–leaf N–leaf P | LLS–SSD

Note: plant ht = plant height; LLS = leaf life span; SLA = specific leaf area; SSD = stem specific density. Modules in our networks are detected using the Spinglass algorithm (see Methods). The modules in this table are the most common modules across the 1,000 networks obtained from the 1,000 bootstrapped trait matrix. The pipe character "|" separates individual modules.

3.2 | Effect of excluding LLS and using area-based leaf N and P on the networks of trait connections

The patterns presented above are largely consistent when excluding LLS – the most gap-filled trait in our dataset (Supporting Information Appendix S1), or when we run the analyses using area-based leaf N and P traits (Supporting Information Appendix S4). The robustness of connections across climates and growth forms is similar in area-based results to that observed in mass-based analyses, with the addition of a connection between LLS–SLA, seed mass–leaf N and seed mass–plant height. In the results excluding LLS, we observe the addition of a connection between SSD–leaf areas. As in the mass-based results, woody species show higher modularity in polar regions when these traits are area-based (Supporting Information Table S5.5, S5.6), and when excluding LLS (Supporting Information Table S2.5, S2.6). As in the mass-based results, no one trait is essential to all networks (as measured by their degree) across all climates for both woody and non-woody growth forms when results are derived using area-based traits (Supporting Information Table S5.7–S5.10), or when we excluded LLS (Supporting Information Table S2.7–2.10). Across leaf nutrient mass-based and area-based results, and results excluding LLS, we are always able to distinguish two modules, one mainly related to LES traits and another one related to reproductive strategy and plant architecture.

4 | DISCUSSION

Here we have identified emergent characteristics of the trait connections for all land plants at a global scale, indicating trait connections both within and across plant leaf, stem and reproductive tissues. Further, we have identified variation in the trait connection network across growth forms (woody and non-woody) and, for the first time (to our knowledge), explicitly accounted for the impact of broad environmental gradients on the trait network. In doing so, our study builds on – and extends – previous attempts that describe the correlations across several traits and several tissue types at global scales (Díaz et al., 2016), and efforts that focused on certain vegetation types (Wright et al., 2007) and narrower environmental gradients (Cheng et al., 2015). The analyses indicate that strong integration across traits across different tissue types exists at the global scale, and across growth forms – however, integration among traits changes across environments. We find that groups of traits cluster forming modules, and that the composition of these modules mostly agrees with previously described trait dimensions. Our analyses also highlight individual traits that are highly connected, as well as robust trait–trait connections that are persistent across growth form and climate regions; however, these results also suggest that the importance of these traits and trait–trait connections are not always supported by current knowledge based on correlative evidence. We found that strong correlations are present as connections, while some weaker correlations are either direct connections or absent as connections. Collectively our analyses of causal connections among traits using a network approach suggest that while the plant phenotype is highly integrated, differences among growth forms and environmental conditions that plants experience modify the strength, clustering and centrality of traits and trait connections in the trait network.

4.1 | Connections among traits across all terrestrial plants

When we compared trait–trait relationships across all land plants using connections and correlations we found that 15% of all the present trait–trait correlations disappear as connections, and the only non-significant trait–trait correlation in the trait network emerged as a connection (leaf N mass–seed mass). These results suggest that trait networks are somewhat sparser than suggested by correlation analyses. That correlations disappear as connections suggests that the interactions among these traits are mediated through another trait(s) in our trait network once the influence of the network is taken into consideration. Importantly, correlations that are critical to plant growth, survival and reproduction – extensively described elsewhere – and which tend to have high correlation values, were always present as connections, whereas only trait–trait correlations with

medium to low values disappear when examined as connections. The correlation between leaf N mass–seed mass was non-existent, yet our analyses suggests there is a direct connection between these traits. This direct connection perhaps arises via the key role that both traits have in plant survival and reproduction or more specifically through the mobilization of vegetative nitrogen needed for the generation of seed storage protein (Shibles & Sundberg, 1998).

Variation in edge density in biological networks has been linked to a compromise between efficiency of connections versus the cost of connection (Alon, 2003; Lipson et al., 2002). At a global scale we found that land plants have a high proportion of connectedness (high trait network edge density) across traits and high integration across tissue types, although not all possible trait connections exist or are strong enough for biological significance. Contrary to our hypothesis, we found no significant differences in the proportion of connection among traits across growth forms, and an overall high proportion of connectedness across traits. This suggests that while there are crucial physiological and anatomical differences across woody and non-woody strategies, these differences do not translate to higher or lower integration of the whole plant phenotype. This supports the idea that matching tissue strategies (i.e. high integration among traits) should be advantageous (Reich, 2014) across growth forms, as this may allow for the efficient acquisition and sharing of resources across the whole plant. On the other hand, our analyses also show that the trait network proportion of connectedness varies across climate regions, suggesting that strong trait coordination and therefore efficient resource sharing comes with a cost and may not be advantageous under all environmental conditions. We, however, reject our hypothesis that traits will be more integrated in water-restricted environments, instead finding some evidence in woody species for lower trait integration in polar regions compared to all other climate regions, and a mixed pattern in non-woody species. Disentangling which abiotic conditions explain the most variation in trait integration, as well as the relationship between trait integration and these leading abiotic variables will be an important next step.

4.2 | Modularity varies across climates

Modules are groups of traits that interact more strongly among themselves, and tend to perform a common function (Alon, 2003); conceptually, modules are similar to trait dimensions/axes (Kleyer et al., 2018). We found there are at least two core modules that are present in both plant growth forms, and a third module present in trait networks of non-woody species. This finding is in agreement with studies describing the dimensionality of plant trait strategies, who usually define at least two independent axes of trait variation (e.g. Ackerly, 2004; Díaz et al., 2016); although up to four or even six independent axes have been described (Jager et al., 2015; Laughlin et al., 2010). Meanwhile, emergent analyses using network approaches have revealed highly integrated trait networks at local and regional scales, concluding a lack of support for the notion of independent trait dimensions (Kleyer et al., 2018; Messier et al., 2017). However, it is important to note that our present study and most other studies that have focused on defining axes of trait variation have asked which traits interact strongly regardless of their tissue type, meanwhile Messier et al. (2017) focused on assessing the modularity of predefined trait dimensions, which is conceptually different. Differences in focus, scale and number as well as type of traits explored may somewhat explain the differences among studies.

SLA, leaf N and leaf P (mass- or area-based) always constituted a module in woody species across climate regions. These three physiological leaf-tissue traits are central to the LES (Wright et al., 2004). Seed mass, plant height and leaf area formed the core traits in a second persistent module (Table 2). These reproductive and architectural traits are relevant to plant size, and plant–water and –light relationships (Moles et al., 2005; Niklas, 1994; Westoby, Falster, Moles, Vesk, & Wright, 2002). Thus, in woody species we have one persistently connected module of traits within a tissue type, and one persistent module of connections of traits that come from different tissue types. Similarly, in non-woody species, leaf N and SLA were always together in one module (leaf P was part of this module, except in tropical climates), while plant height and leaf area were together in a separate module (SSD formed part of this module except in polar climates). The importance of these two modules in the strategies of plants is supported by the LES and the global spectrum of plant form and function (Díaz et al., 2016; Reich et al., 1999, 1997). Thus, much in agreement with studies focusing on defining the dimensionality of plant strategies, we find the trait network has one module whose function is carbon uptake represented by leaf physiological traits, and a second module whose function is more related to plant reproductive and architectural traits. While trait networks are integrated to maximize the efficiency of resource use and acquisition as suggested by Reich (2014) and supported by our centrality analyses and others (e.g. Kramer-Walter et al., 2016; Messier et al., 2017), trait networks are at the same time segregated into modules of more highly interacting traits that may provide adaptive advantages under varying environmental conditions.

The degree of modularity of trait networks varies across environmental gradients for woody, but not for non-woody species. This suggests plant growth forms differ in their strategies to cope with environmental conditions. The lack of variation in the modulatory of non-woody species across environments suggests they experience weaker environmental filtering compared to woody species (Šímová et al., 2018). Weaker environmental filtering in non-woody species perhaps results from their shorter life span, dormancy (and other bet-hedging) strategies and lack of long-persisting, reinforced stems above ground, which in combination may allow them to avoid much environmental heterogeneity. Within woody species, modularity is greater in polar than in tropical or temperate climates, meaning that modules in the trait network in polar regions are more independent from one another compared to other climate regions. This suggests that less coordination between trait dimensions (modules) is advantageous in polar environments. Higher independence among modules in polar regions may give plants more flexibility to adjust functions and help better manage risk of component failure (Gilarranz, Rayfield,

Liñán-Cembrano, Bascompte, & Gonzalez, 2017). This may be in response to greater variation in water availability between seasons (Feddema, 2005), greater temporal asynchrony between resources in polar environments, narrower range of variation in traits under harsher environmental conditions making relationship between traits weaker and thus increasing modularity (e.g. de la Riva et al., 2018), or more variable and/or different selection forces acting more strongly on each independent trait module (Laughlin et al., 2010).

4.3 | Highly connected traits

High centrality – having a high number of connections to other units in a network – suggests that a variable tends to be influential in terms of regulating critical functions or be involved in the regulation of more functions, thereby having greater impact on higher level properties such as fitness (Koschützki & Schreiber, 2008). LLS and SSD were the traits with most connections to other traits across land plants. Indeed, LLS is a crucial trait in the resource acquisition strategy of plants, influencing the carbon construction cost and carbon gain of leaves (Reich et al., 1999, 1992), while SSD impacts plant hydraulic and mechanical properties and influences the nutrient, carbon and water economy of stems (Chave et al., 2009). Further, variation in these traits has been shown to impact growth and fecundity (Adler et al., 2014), and also to contribute to the structuring of woody communities (Kunstler et al., 2016) and to influence ecosystem level processes (Reich, 2014; Reich et al., 1997). However, trait centrality was labile within growth forms across climate regions. Changes in the centrality of traits across growth forms and climate regions may simply reflect the scale-dependent nature of the selective, genetic and biophysical forces acting on traits. We conjecture that trait centrality may indeed reflect some of the functional relevance of traits in the trait network, thus providing crucial information about what traits are critical to the definition and understanding of plant strategies.

4.4 | Trait connections across growth forms and climate regions

Connections between seed mass–leaf area, leaf N–SLA, leaf P–leaf N and plant height–leaf area stand out because they were always present in analyses of growth forms, and across different climate types (Table 3). Some of these connections are well known (e.g. leaf N–SLA, leaf P–leaf N), and previous correlation analyses have identified their importance in understanding compromises among traits and their impact on plant function (Reich et al., 1999, 1992, 1997; Wright et al., 2004). However, some others are connections that previous correlation analyses suggested have no or weak relationships across habitats, and therefore their importance has been downplayed (e.g. seed mass–leaf area, plant height–leaf area; Table 3). In the first case – where we detect a connection and previous studies show a strong correlation – evidence suggests that these connections are maintained through selective pressure of biophysical constraints and natural selection (Table 3). For example, an increase in SLA will generally be linked to an increase in concentration of leaf N and other cytoplasmic molecules (Meziane & Shipley, 2001; Reich et al., 1997). At the same time, natural selection reinforces a strong relationship between SLA and leaf N through processes such as herbivory and competition (Reich et al., 1997), limiting the trait space where optimal combinations of these traits occur. In the second case – where conditional dependency between two traits exists, but previous correlation tests suggested a weak relationship – we propose that these trait connections are maintained in the plant phylogeny through neutral or selective processes, but contradictory selective forces across habitats weaken the correlation among these traits. Some studies have reported a triangular relationship between seed mass and leaf area in temperate woody species (i.e. big leaves have big or small seeds, but small leaves only have small seeds; Cornelissen, 1999); other studies report positive rather than triangular relationships across woody sclerophyll species (Westoby & Wright, 2003), while others show no relationship among these traits across woody tropical species (Wright et al., 2007). In both cases, our analyses suggest that these trait connections are robust after accounting for all other traits, and across climates and growth forms, but the forces maintaining these connections might differ.

Some well-known, strong trait–trait correlations across plants stand out because they do have robust connections globally but not across growth forms or climate regions in our study. For instance, the connection between SLA–LLS is direct in the global data and in woody plants but not in non-woody plants. Moreover, this connection was observed in four of five climate regions for woody plants, but only one of five for non-woody plants. This weaker connection in subsets of the global data could suggest that although a strong correlation exists between these two traits, the connection between these traits could be mechanistically mediated through other traits in some cases, or the connection only exists when the absolute range in LLS is large, as is the case for woody plants. Additionally, given that the vast majority of global data on LLS for graminoids likely reflects longevity of the entire leaf blade (much of which may be senescing or dead) rather than of active photosynthetic tissue per se (Craine, Berin, Reich, Tilman, & Knops, 1999; Craine & Reich, 2001), the majority of global data on graminoid LLS may not be as comparable to LLS in woody and non-woody dicots as the research community recognizes (or wishes). This may contribute to differences in connection of SLA–LLS in woody versus non-woody plants.

Previous plant trait studies have focused on understanding the interdependence between pairs of traits or among multiple traits using correlation analyses in combination with ordination techniques (e.g. Supporting Information Table S1.2. These studies have shown that the strength and form of the relationships between traits among co-occurring species vary across environments (Ackerly, 2004; Reich et al., 1999), and among functional groups (Reich et al., 2003), with axes of trait variation shifting, collapsing or arising across environmental gradients and different growth forms. The analyses presented here suggest that direct and indirect interactions among traits within and between tissue types also shift across growth forms and climate regions. We found that LLS and SSD are the most central traits globally, but were not always connected within all climate

TABLE 3 Trait connections that are robust (i.e. common across groups) across growth forms and climate regions and proposed mechanisms that maintain this connection

Robust connection	Woody/non-woody	Woody across climate	Non-woody across climate	Mechanisms	Details
Leaf P–leaf N	.62	.51–.70	.47–.72	Biochemical and biogeochemical constraints. Selection through competition and herbivory	Selection through biochemical constraints reinforced through compromises between allocation of resources to metabolism (investment in genetic material especially ribosomal RNA) versus growth (investment in proteins); biogeochemical constraints mediated by adaptation/acclimation to soil conditions; unviable/low fitness strategies may be selected out by herbivory and competition based processes (Kerkhoff, Fagan, Elser, & Enquist, 2006; Reich, 2014; Reich & Oleksyn, 2004)
SLA–leaf N	.52–.64	.59–.67	.41–.57	Biophysical constraint; selection of viable strategies through competition and herbivory	Changes in leaf N results from increases in LMA, increase in SLA results in an increase in cytoplasmic compounds, including N; structural investment, competition and herbivory select certain combinations of these traits (Meziane & Shipley, 2001; Reich et al., 1999, 1992, 1997)
Plant height–leaf area	.50–.54	.29–.57	.36–.70	Biophysical constraint	Decrease in leaf size with increasing light demands correlates weakly, selection through light competition in certain florae; small trunks with big leaves are physically unviable; large-leaf crown is more efficient because it requires less woody support investment (Givnish, 1979; Niinemets & Kull, 1994; Niklas, 1994)
Seed mass–leaf area	.41–.42	.15–.50	.36–.41	Unclear if this correlation is general across floras or what maintains it. Possible controls by biophysical constraints or vascular/meristematic demands	Correspondence between axis and appendage size (Corner's rule). Triangular relationship – plants with big leaves can have either very small or large seeds, but plants with small leaves only have small seeds in woody European species; positive but not triangular relationship in sclerophyll vegetation in Australia; no relationship among these traits in tropical forests in the Americas (Cornelissen, 1999; Westoby & Wright, 2003; Wright et al., 2007)

Note: LMA = leaf mass per area; SLA = specific leaf area. The range of R^2 values observed across growth form, and then by growth form across climate regions in this study is provided in the second to fourth columns. We provided proposed mechanisms that maintain these trait connection as well as specific hypothesis about each mechanism (Details column).

zones, especially for non-woody plants (but see above); moreover, few trait–trait connections exist robustly across all growth forms and climate gradients (Table 3). Despite the difference in statistical approach compared with previous research (e.g. Ackerly, 2004; Fortunel et al., 2012; Kramer-Walter et al., 2016), our study supports the existence of two distinguishable dimensions or functional modules across land plants and climate regions. One module is related to physiological leaf traits related to carbon uptake and economy, and another related to reproductive strategy and plant architecture. The findings presented here contribute to the fundamental understanding of dependencies between plant traits and their variation across environmental gradients. Our approach represents an important step forward on the collective path to understanding the causal links among multiple traits across multiple tissue types, and within and across different climate zones and plant growth forms.

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DATA AVAILABILITY STATEMENT

The data used for the analyses are publicly available: climate zones (https://webmap.ornl.gov/ogc/wcsdown.jsp?dg_id=10012_1) and plants (www.try-db.org; upon request to TRY).

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BIOSKETCH

Habacuc Flores-Moreno undertook this research as a post-doc in Peter Reichs' lab at the University of Minnesota. His work focuses on linking the role of plant functional traits to community and ecosystem processes in different environmental and ecological contexts.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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APPENDIX

DATA SOURCES: LIST OF STUDIES INCLUDED IN THE SUBSET OF THE TRY DATABASE USED IN THE CURRENT STUDY

Adler, P. B., Milchunas, D. G., Lauenroth, W. K., Sala, O. E., & Burke, I. C. (2004). Functional traits of graminoids in semi-arid steppes: A test of grazing histories. *Journal of Applied Ecology*, *41*(4), 653–663.

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